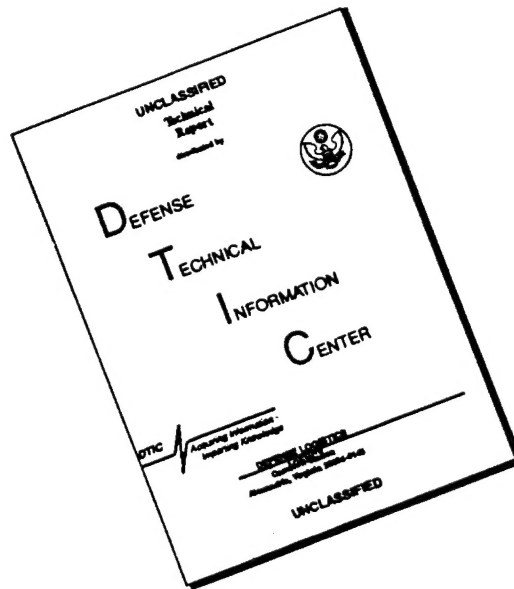


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Time Dependence of Visual Deprivation: A Comparison between Models Of Plasticity and Experimental Results

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Abstract

Receptive fields in the visual cortex can be altered by changing the visual environment, as has been shown many times in deprivation experiments. In this paper we simulate this set of experiments using two different models of cortical plasticity, BCM and PCA. The visual environment used is composed of natural images for open eye and of noise for closed eyes. We measure the response of the neurons to oriented stimuli, and use the time course information of the neuronal response to provide a preliminary quantitative comparison between the cortical models and experiment.

1 Introduction

Two important characteristics of the visual response of most neurons in cat striate cortex are that they are binocular and show a strong preference for contours of a particular orientation (Hubel and Wiesel, 1962). Although some orientation selectivity exists in striate cortex prior to visual experience, maturation to adult levels of specificity and responsiveness requires normal contour vision during the first 2 months of life. (Albus and Wolf, 1984; Barlow, 1975; Blakemore and Van-Sluyters, 1975; Bonds, 1975; Braastad and Heggelund, 1985; Frégnac and Imbert, 1978; Frégnac and Imbert, 1984; Movshon and van Sluyters, 1981)

Ocular dominance is a measure of how effectively the neuron can be driven through the left and right eyes, respectively. Up to the level of the LGN, visual information originating from the two eyes is segregated in separate pathways, striate cortex is thus the first site where individual cells receive afferent projections from both left and right eyes, and in normal kitten striate cortex most of the visually responsive cells are binocular.

One of the most dramatic examples of cortical plasticity is the alteration of ocular dominance in kitten striate cortex in monocular deprivation, a procedure in which, one eye is deprived of patterned stimuli (by either suturing the eyelid closed or using an eye patch). In such an imbalanced visual environment, cells in kitten's striate cortex change from mostly binocular to almost exclusively monocular: in less than 24 hours most cells lose their responsive to stimulation through the deprived eye and can only be driven through the eye that remains open (Blakemore and van Sluyters, 1974; Olson and Freeman, 1975; Wiesel and Hubel, 1963).

The change induced by monocular deprivation is reversible. In the rearing condition called reverse suture there is an initial period of monocular deprivation: after the cortical neurons have become monocular, the deprived eye is opened and the other eye closed. In this situation the cortical neurons lose responsiveness to the newly closed eye, and become responsive to the newly opened eye (Blakemore and van Sluyters, 1974). Acute studies indicate that, as the ocular dominance of cortical responsiveness shifts from one eye to the other, there is rarely a period when cells can be strongly and equally activated by both eyes (Movshon, 1976; Mioche and Singer, 1989).

In this paper we model this set of experiments, looking specifically at the time course of neuronal response during visual deprivation. In this way we wish to directly compare two different learning rules with each other,

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and also with experiment. The visual environment to which open eyes are exposed is assumed to be composed of preprocessed natural images, whereas closed eyes receive noise as their inputs. The architecture assumed in these models is of single learning neurons, as a first step to understanding the behavior of networks.

We compare the two learning rules BCM (Bienenstock et al., 1982; Intrator and Cooper, 1992) and PCA (Oja, 1982). Both of these rules have been shown to develop orientation selectivity in a realistic visual environment (Law and Cooper, 1994; Shouval and Liu, 1994). For binocular misaligned inputs BCM develops cells with varying degrees of binocularity whereas PCA develops only perfectly binocular cells (Shouval et al., 1996). Previous simulations of the deprivation experiments have been performed using simplified inputs for the BCM theory (Clothiaux et al., 1991). In this paper we use realistic inputs.

2 Methods

To model the normal visual environment, we use 24 gray-scale images with the dimensions 256×256 pixels. The inputs to the retinas are processed with a retinal like center-surround receptive field, which we approximate as a difference of two Gaussians. The receptive fields are restricted to finite circular patches of radius $R_r = 13$. Thus in each iteration a different circular patch is chosen randomly as input to the neuron. The exact time course of these simulations is dependent on the parameters chosen; we have therefore examined these over a large parameter regime. At each set of parameters we performed all of the deprivation simulations, and compared their timing ratios, in order to test the robustness of our predictions. Examples of the simulations are shown in Figures 1 and 2 for BCM and PCA respectively.

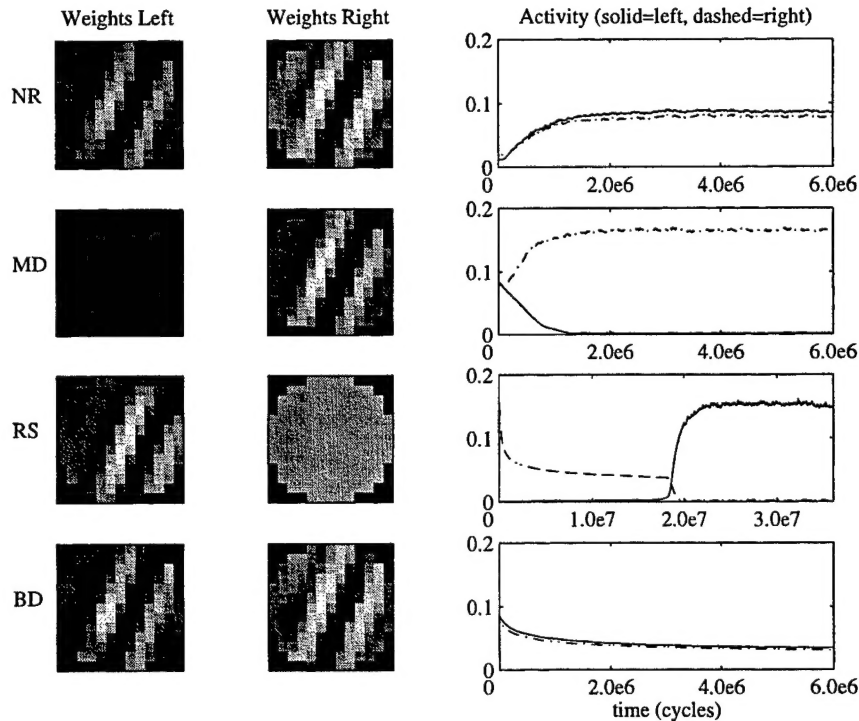


Figure 1: Example BCM Simulations. Left: Final weight configuration. Right: Maximum response to oriented stimuli, as a function of time. Simulations from top to bottom are as follows. Normal Rearing (NR): both eyes presented with patterned input. Monocular Deprivation (MD): following NR, one eye is presented with noisy input and the other with patterned input. Reverse Suture: following MD, the eye given noisy input is now given patterned input, and the other eye is given noisy input. Binocular Deprivation (BD): following NR, both eyes are given noisy input. It is important to note that if Binocular Deprivation is run longer, selectivity will eventually be lost

We chose the modification rule for the BCM simulations to be quadratic, $\dot{\mathbf{m}} = \eta\phi(c, \theta)\mathbf{d} = \eta c(c - \theta)\mathbf{d}$,

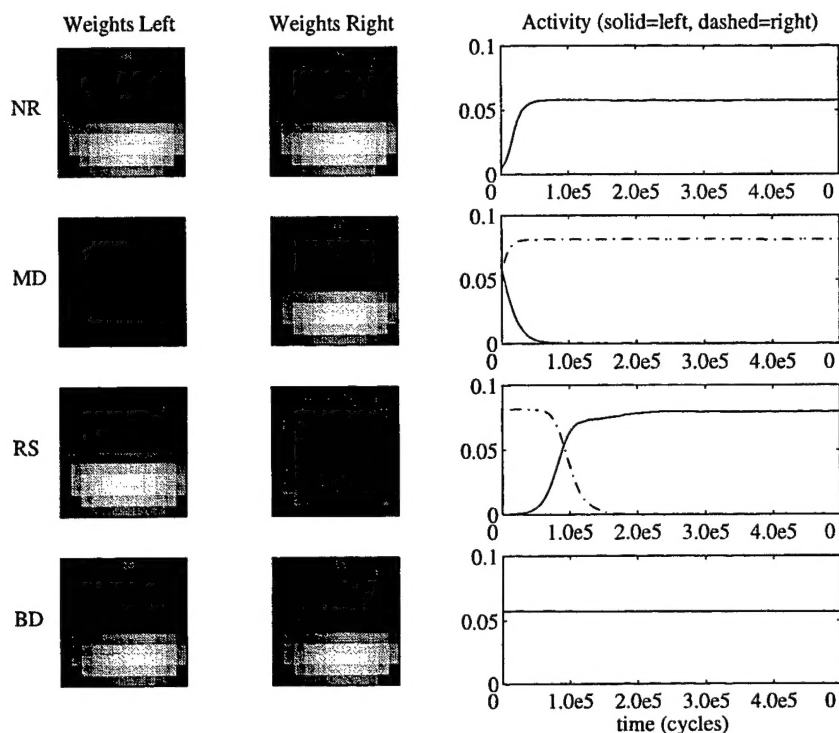


Figure 2: Example PCA Simulations. Left: Final weight configuration. Right: Maximum response to oriented stimuli, as a function of time. Simulations from top to bottom are as follows. Normal Rearing (NR): both eyes presented with patterned input. Monocular Deprivation (MD): following NR, one eye is presented with noisy input and the other with patterned input. Reverse Suture: following MD, the eye given noisy input is now given patterned input, and the other eye is given noisy input. Binocular Deprivation (BD): following NR, both eyes are given noisy input.

where the output is the simple dot product of the input and weight vectors, passed through a sigmoid function, $c = \sigma(\mathbf{d} \cdot \mathbf{m})$. The precise time course of the neuron activity is dependent on the choice of the functional form of both the modification function, ϕ , and the sigmoid. Variations of these are currently being investigated.

We measure the response $Y(t)$ of the neurons using oriented stimuli. Of particular interest is characteristic half-rise (half-fall) time for the growth (decay) of neuronal response, referred to as either $t_{1/2}$ or simply \mathcal{T} . An example of this is shown in Figure 3.

The half-time measurement provides a direct comparison between the BCM and PCA models. It also provides a way to quantitatively translate between simulation cycles and real time, yielding a quantitative comparison with experiment.

3 Results

Summary of Experimental Results

The following table summarizes the experimental results to which we can compare the two models. The exact results depend on when in the critical period the experiments were done. The results allow us to estimate the values of the activity half-rise time, $\mathcal{T}_{\text{rise}}$, or half-fall time, $\mathcal{T}_{\text{fall}}$ whichever is appropriate for the particular experiment.

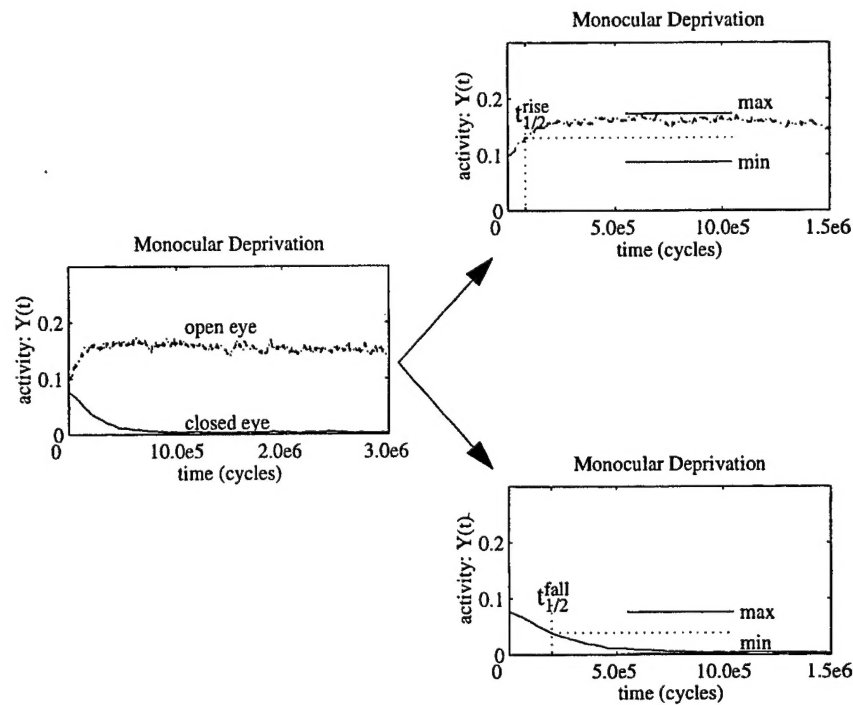


Figure 3: Example of a Response Half-Time Measurement. This is an illustration of the procedure for measuring the half-times. Though the example uses a BCM simulation, the specific numbers are not important. The time is measured for the neuron to either rise or fall, half way between its minimum and maximum responses.

Summary of Experimental Results		
Experiment	Reference	Half-Time \mathcal{T}
Monocular Deprivation	<ul style="list-style-type: none"> • OD changes were observed as early as 6 h(Freeman and Olson, 1982; Mioche and Singer, 1989) • complete loss of response to closed as early as 12 h(Mioche and Singer, 1989) • moderate increase of response to the normal eye occasionally(Mioche and Singer, 1989) 	$\mathcal{T}_{\text{fall}}^{\text{MD}} \approx 6\text{-}12 \text{ h}$
Binocular Deprivation	<ul style="list-style-type: none"> • cortical response reduced within 3 d(Freeman et al., 1981) 	$\mathcal{T}_{\text{fall}}^{\text{BD}} < 3 \text{ d}$
Reverse Suture	<ul style="list-style-type: none"> • the time course for the reduction of response to the newly deprived eye was similar to monocular deprivation(Mioche and Singer, 1989) • At least 24 h of reverse suture is required before the responses to the deprived eye reappears(Mioche and Singer, 1989) 	$\mathcal{T}_{\text{fall}}^{\text{RS}} \approx \mathcal{T}_{\text{fall}}^{\text{MD}}$ $\mathcal{T}_{\text{rise}}^{\text{RS}} \approx 1\text{-}4 \text{ d}$

It will be more useful to look at *ratios* of these times, so we can make a reasonable comparison with the theory. The above values of \mathcal{T} give us the following ratios, that we can then use in our comparison.

- $\mathcal{T}_{\text{fall}}^{\text{RS}} / \mathcal{T}_{\text{fall}}^{\text{MD}} \approx 1$
- $2 < \mathcal{T}_{\text{rise}}^{\text{RS}} / \mathcal{T}_{\text{fall}}^{\text{MD}} < 16$
- $0.33 < \mathcal{T}_{\text{rise}}^{\text{RS}} / \mathcal{T}_{\text{fall}}^{\text{BD}} < 16$

PCA Results

We can use the full time-domain solution (Wyatt and Elfadel, 1995) of the PCA equations in order to explore the deprivation simulations analytically. The full detail of these calculations is given in the Appendix. The solutions are in terms of the covariance matrix of the input and the initial conditions, however it is difficult to give analytical results for the half-times, \mathcal{T} , of the deprivation simulations. One can, however, make some predictions about the general characteristics of these times. Expanding the initial weight vector in terms of the eigenvectors (\mathbf{v}_j) of the natural scene covariance matrix, $\mathbf{m}_0 = \sum_j \begin{pmatrix} a_j^l \mathbf{v}_j \\ a_j^r \mathbf{v}_j \end{pmatrix}$, adding the assumption that natural scenes are dominated by the first eigenvector of the covariance matrix, \mathbf{v}_1 with eigenvalue λ_1 , and taking appropriate time limits (see Appendix A), we obtain the following equations for the time development of the weights

$$\mathbf{m}^{\text{NR}}(t) = \frac{\sum_j \frac{1}{2} \begin{pmatrix} \mathbf{v}_j [(a_j^l + a_j^r)e^{2\lambda_j t} + (a_j^l - a_j^r)] \\ \mathbf{v}_j [(a_j^l + a_j^r)e^{2\lambda_j t} + (a_j^r - a_j^l)] \end{pmatrix}}{\left(\frac{1}{2} \sum_j [(a_j^l + a_j^r)^2 e^{4\lambda_j t} + (a_j^l - a_j^r)^2] + 1 - \sum_j [(a_j^l)^2 + (a_j^r)^2] \right)^{1/2}} \quad (3.1)$$

$$\mathbf{m}^{\text{MD}}(t) = \frac{\begin{pmatrix} e^{\lambda_1 t} \mathbf{v}_1 \\ e^{\sigma^2 t} \mathbf{v}_1 \end{pmatrix}}{(e^{2\lambda_1 t} + e^{2\sigma^2 t})^{1/2}} \quad (3.2)$$

$$\mathbf{m}^{\text{BD}}(t) = \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix} \quad (3.3)$$

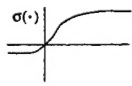
$$\mathbf{m}^{\text{RS}}(t) = \frac{\begin{pmatrix} e^{\sigma^2 t} \mathbf{v}_1 \\ e^{\lambda_1 t} \epsilon \mathbf{v}_1 \end{pmatrix}}{(e^{2\sigma^2 t} + \epsilon e^{2\lambda_1 t})^{1/2}} \quad (3.4)$$

Comparing the MD and RS solutions (Equations 3.2 and 3.4) one sees that the times for the decay and recovery of neuronal activity must be identical for each regardless of noise levels and input statistics. Therefore the PCA model predicts correctly the time for the neuronal activity to fall in these deprivation situations, but fails to properly predict the time for the recovery of activity in RS compared to MD.

Equation 3.3 implies that a neuron following Oja's rule, experiencing binocular deprivation following normal rearing, performs a random walk about the normal reared state. Thus PCA is again inconsistent with the experiment results.

BCM Results

In order to determine the dependence of the response half-times on model and input parameters we need to perform simulations over a range of those parameters and measure the time \mathcal{T} for each of these. The response half-times for each deprivation experiment depend on the parameters in different ways, so it is possible to find a parameter regime which yields consistent time ratios. The parameter regime is initially chosen to give *stable* simulations, and then explored more finely to determine regions with consistent time ratios. Stability is lost if the learning rate is too large, or if the memory constant, τ , is too large causing BCM sliding threshold, θ to move too slowly.

Parameters for BCM Simulations	
Learning Rule	$\dot{\mathbf{m}} = \eta c(c - \theta) \mathbf{d}$ $\dot{\theta} = \frac{1}{\tau}(c^2 - \theta)$
Activation Rule	$c = \sigma(\mathbf{m} \cdot \mathbf{d})$
cortical sigmoid	 $\begin{cases} \sigma(-\infty) = -1 \\ \sigma(+\infty) = 50 \end{cases}$
Initial threshold	$\theta_0 = 0.73$
Input mean	$\langle \mathbf{d} \rangle = -3.3 \cdot 10^{-5}$
Input variance	$\text{var}(\mathbf{d}) = 1.0$
RF Diameter	13 pixels
Retinal DOG ratio	3:1
Learning rate	$\eta = 5 \cdot 10^{-7}, \dots, 5 \cdot 10^{-5}$
Memory constant	$\tau = 10, \dots, 3510$
Noise Levels	uniform noise= [-.25:.25], ..., [-2.5,2.5]

The two most important parameters are the noise level to the closed eye and the memory constant, τ . Figure 4 shows the results of varying these two parameters. We see that while the noise level has a dramatic effect on the time course of the neuronal response, the memory constant has surprisingly little effect. This may indicate a striking difference between the natural scene environment and previous work done with abstract inputs (Clothiaux et al., 1991), where the memory constant played a more important role in the timing.

We see from Figure 4 that the dependence on the noise level is different for each deprivation simulation. This allows us to possibly locate a range of noise levels for which the relative times are consistent with experiment. Figure 5 displays all of the parameter points explored, and which ones yielded time ratios consistent with *all* of the experimentally determined ratios.

4 Summary and Conclusions

It has been demonstrated that the PCA rule fails to account for the time course of the deprivation experiments in a manner consistent with the experiment. Most dramatic is the result that binocular deprivation to a PCA neuron gives only a random walk response. BCM on the other hand can account for the time course, within a particular parameter regime. This parameter regime can be summarized by the range of 3 parameters:

- memory constant $\tau = 500, \dots, 3000$
- learning rate $\eta = 4.5 \cdot 10^{-6}, \dots, 6 \cdot 10^{-6}$
- noise level $\sigma = 0.88, \dots, 1.4$ (or [-1.1:1.1], ..., [-1.45:1.45])

Note that the valid parameter regime is *not* defined by a sharp boundary, but that near the edge the system is less robust.

One of the features of this approach is the direct calculation of the model parameters in terms of experimental quantities. Using the range of half-time values exhibited across the valid parameter regime for, say, monocular deprivation, and attributing that range to the known 6-12 hour range obtained from experiment, we can find a range for the possible values of τ in minutes. Doing this we find that τ ranges between 1-15 minutes. We are investigating how this might be affected by the slope of the modification function, ϕ , at threshold and the form of the cortical sigmoid. A final determination of the allowed values of τ may give us clues to the cellular and molecular processes involved.

A Classical Rearing Conditions: PCA Analysis

The Wyatt solution is the explicit time-domain solution of Oja's equation for a single neuron

$$\dot{\mathbf{m}} = c(\mathbf{d} - c\mathbf{m})$$

This solution is given in terms of the initial weight vector, \mathbf{m}_0 , and the covariance matrix of the input, \mathbf{C} by the expression:

$$\mathbf{m}(t) = \frac{e^{Ct}\mathbf{m}_0}{\left(\|e^{Ct}\mathbf{m}_0\|^2 + 1 - \|\mathbf{m}_0\|^2\right)^{1/2}} \quad (\text{A.5})$$

In this section we use the Wyatt solution to determine the time dynamics of a neuron following Oja's learning rule in an environment modeling the classical visual cortical plasticity experiments.

Some notation:

single eye input vectors: $\mathbf{d}^l \equiv$ left eye inputs, $\mathbf{d}^r \equiv$ right eye inputs

single eye covariance matrix: $\mathbf{C} \equiv \langle \mathbf{d}\mathbf{d}^T \rangle$

full input vector: $\mathbf{D} \equiv \begin{pmatrix} \mathbf{d}^l \\ \mathbf{d}^r \end{pmatrix}$

full covariance matrix: $\mathbf{C} \equiv \langle \mathbf{D}\mathbf{D}^T \rangle = \left\langle \begin{pmatrix} \mathbf{d}^l \\ \mathbf{d}^r \end{pmatrix} ((\mathbf{d}^l)^T \ (\mathbf{d}^r)^T) \right\rangle$
 $= \begin{pmatrix} \mathbf{C}^{ll} & \mathbf{C}^{lr} \\ \mathbf{C}^{rl} & \mathbf{C}^{rr} \end{pmatrix}$

natural scene (single eye) covariance matrix:
eigenvectors/values of covariance matrix:

$$\mathbf{C}\mathbf{v}_j = \lambda_j \mathbf{v}_j \quad (j = 1, \dots, n)$$

$$\mathbf{v}_i^T \mathbf{v}_j = \delta_{ij}$$

$$\lambda_1 > \lambda_2 > \dots > \lambda_n$$

(assumption) noise (single eye) covariance matrix:

$$\sigma^2 = \begin{pmatrix} \sigma^2 & & \mathbf{0} \\ & \ddots & \\ \mathbf{0} & & \sigma^2 \end{pmatrix}$$

The rearing experiments in this new notation are as follows:

Experiment	initial weight vector	full covariance matrix
Normal Rearing (NR)	\mathbf{m}_0^{NR}	$\begin{pmatrix} \mathbf{C} & \mathbf{C} \\ \mathbf{C} & \mathbf{C} \end{pmatrix}$
Monocular Deprivation (MD)	$\mathbf{m}_0^{\text{MD}} = \mathbf{m}^{\text{NR}}(t \rightarrow \infty)$	$\begin{pmatrix} \mathbf{C} & \mathbf{0} \\ \mathbf{0} & \sigma^2 \end{pmatrix}$
Binocular Deprivation (BD)	$\mathbf{m}_0^{\text{BD}} = \mathbf{m}^{\text{NR}}(t \rightarrow \infty)$	$\begin{pmatrix} \sigma^2 & \mathbf{0} \\ \mathbf{0} & \sigma^2 \end{pmatrix}$
Reverse Suture (RS)	$\mathbf{m}_0^{\text{RS}} = \mathbf{m}^{\text{MD}}(t \rightarrow \infty)$	$\begin{pmatrix} \sigma^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{C} \end{pmatrix}$

The general procedure will be the following:

- expand the initial weight vector \mathbf{m}_0 in terms of the eigenvectors of the covariance matrix (\mathbf{v}_j).
- plug into the Wyatt solution (Equation A.5) to obtain $\mathbf{m}(t)$. We will have to use the full covariance matrix \mathbf{C} instead of the single eye covariance matrix \mathbf{C} .
- add approximations to simplify the expression

We present each rearing condition currently.

Normal Rearing (NR)

- expand the initial weight vector \mathbf{m}_0 in terms of the eigenvectors of the covariance matrix (\mathbf{v}_j) .

$$\mathbf{m}_0 = \begin{pmatrix} \mathbf{m}_0^l \\ \mathbf{m}_0^r \end{pmatrix} = \sum_j \begin{pmatrix} a_j^l \mathbf{v}_j \\ a_j^r \mathbf{v}_j \end{pmatrix}$$

- plug into the Wyatt solution (Equation A.5) to obtain $\mathbf{m}(t)$

We need to do this part in steps, calculating $\mathcal{C}\mathbf{m}_0$ first, then calculating each term in Equation A.5.

$$\begin{aligned} \mathcal{C}\mathbf{m}_0 &= \begin{pmatrix} \mathcal{C} & \mathcal{C} \\ \mathcal{C} & \mathcal{C} \end{pmatrix} \sum_j \begin{pmatrix} a_j^l \mathbf{v}_j \\ a_j^r \mathbf{v}_j \end{pmatrix} = \sum_j \begin{pmatrix} \lambda_j(a_j^l + a_j^r) \mathbf{v}_j \\ \lambda_j(a_j^l + a_j^r) \mathbf{v}_j \end{pmatrix} \\ &= \sum_j \lambda_j(a_j^l + a_j^r) \begin{pmatrix} \mathbf{v}_j \\ \mathbf{v}_j \end{pmatrix} \\ \mathcal{C}^2\mathbf{m}_0 &= \begin{pmatrix} \mathcal{C} & \mathcal{C} \\ \mathcal{C} & \mathcal{C} \end{pmatrix} \sum_j \lambda_j(a_j^l + a_j^r) \begin{pmatrix} \mathbf{v}_j \\ \mathbf{v}_j \end{pmatrix} \\ &= \sum_j 2\lambda_j^2(a_j^l + a_j^r) \begin{pmatrix} \mathbf{v}_j \\ \mathbf{v}_j \end{pmatrix} \\ &\vdots \\ \mathcal{C}^i\mathbf{m}_0 &= \sum_j 2^{i-1}\lambda_j^i(a_j^l + a_j^r) \begin{pmatrix} \mathbf{v}_j \\ \mathbf{v}_j \end{pmatrix} \\ &\vdots \end{aligned}$$

$$\begin{aligned} e^{\mathcal{C}t}\mathbf{m}_0 &= \left(1 + (\mathcal{C}t) + \frac{(\mathcal{C}t)^2}{2!} + \dots\right) \mathbf{m}_0 \\ &= \sum_j \left\{ (a_j^l + a_j^r) \begin{pmatrix} \mathbf{v}_j \\ \mathbf{v}_j \end{pmatrix} \left(1 + \lambda_j t + \frac{2\lambda_j^2 t^2}{2!} + \dots + \frac{2^{i-1}\lambda_j^i t^i}{i!} + \dots\right) - \begin{pmatrix} a_j^r \mathbf{v}_j \\ a_j^l \mathbf{v}_j \end{pmatrix} \right\} \\ &= \sum_j \frac{1}{2} \begin{pmatrix} \mathbf{v}_j [(a_j^l + a_j^r)e^{2\lambda_j t} + (a_j^l - a_j^r)] \\ \mathbf{v}_j [(a_j^l + a_j^r)e^{2\lambda_j t} + (a_j^r - a_j^l)] \end{pmatrix} \end{aligned}$$

$$\|\mathbf{m}_0\|^2 = \mathbf{m}_0^T \mathbf{m}_0 = \sum_j [(a_j^l)^2 + (a_j^r)^2]$$

$$\begin{aligned} a_{j+} &\equiv (a_j^l + a_j^r) \\ a_{j-} &\equiv (a_j^l - a_j^r) \\ \|e^{\mathcal{C}t}\mathbf{m}_0\|^2 &= \sum_j \frac{1}{4} [a_{j+}^2 e^{4\lambda_j t} + a_{j-}^2 + 2a_{j-}a_{j+} e^{2\lambda_j t} + a_{j+}^2 e^{4\lambda_j t} + a_{j-}^2 - 2a_{j-}a_{j+} e^{2\lambda_j t}] \\ &= \frac{1}{2} \sum_j [(a_j^l + a_j^r)^2 e^{4\lambda_j t} + (a_j^l - a_j^r)^2] \end{aligned}$$

which brings us to our solution for normal rearing

$$\mathbf{m}^{\text{NR}}(t) = \frac{\sum_j \frac{1}{2} \begin{pmatrix} \mathbf{v}_j [(a_j^l + a_j^r)e^{2\lambda_j t} + (a_j^l - a_j^r)] \\ \mathbf{v}_j [(a_j^l + a_j^r)e^{2\lambda_j t} + (a_j^r - a_j^l)] \end{pmatrix}}{\left(\frac{1}{2} \sum_j [(a_j^l + a_j^r)^2 e^{4\lambda_j t} + (a_j^l - a_j^r)^2] + 1 - \sum_j [(a_j^l)^2 + (a_j^r)^2] \right)^{1/2}} \quad (\text{A.6})$$

- add approximations to make the equations simpler

The $t \rightarrow \infty$ limiting case, needed for the calculations in the next few sections, is straightforward to calculate. If the largest eigenvalue is non-degenerate, then \mathbf{m} will become

$$\mathbf{m}^{\text{NR}}(t \rightarrow \infty) = \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix}$$

Monocular Deprivation (MD)

- expand the initial weight vector \mathbf{m}_0 in terms of the eigenvectors of the covariance matrix (\mathbf{v}_j) .

Since we are starting from the $\mathbf{m}^{\text{NR}}(t \rightarrow \infty)$ state, the initial weight vector for monocular deprivation is already in terms of the eigenvectors of the covariance matrix.

$$\mathbf{m}_0 = \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix}$$

- plug into the Wyatt solution (Equation A.5) to obtain $\mathbf{m}(t)$.

$$\begin{aligned} C\mathbf{m}_0 &= \begin{pmatrix} \mathbf{C} & \mathbf{0} \\ \mathbf{0} & \sigma^2 \end{pmatrix} \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix} = \sqrt{\frac{1}{2}} \begin{pmatrix} \lambda_1 \mathbf{v}_1 \\ \sigma^2 \mathbf{v}_1 \end{pmatrix} \\ e^{Ct}\mathbf{m}_0 &= \sqrt{\frac{1}{2}} \begin{pmatrix} e^{\lambda_1 t} \mathbf{v}_1 \\ e^{\sigma^2 t} \mathbf{v}_1 \end{pmatrix} \\ \|\mathbf{m}_0\|^2 &= 1 \\ \|e^{Ct}\mathbf{m}_0\|^2 &= \frac{1}{2}(e^{2\lambda_1 t} + e^{2\sigma^2 t}) \end{aligned}$$

which yields

$$\mathbf{m}^{\text{MD}}(t) = \frac{\begin{pmatrix} e^{\lambda_1 t} \mathbf{v}_1 \\ e^{\sigma^2 t} \mathbf{v}_1 \end{pmatrix}}{(e^{2\lambda_1 t} + e^{2\sigma^2 t})^{1/2}} \quad (\text{A.7})$$

- add approximations to make the equations simpler

The assumption we are going to make is that $\lambda_1 > \sigma^2$. This is reasonable, because the noise to the closed eye should be smaller than the eigenvalue from the natural scene covariance. With this assumption, the $t \rightarrow \infty$ limiting case becomes

$$\mathbf{m}^{\text{MD}}(t \rightarrow \infty) = \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{0} \end{pmatrix}$$

Binocular Deprivation (BD)

- expand the initial weight vector \mathbf{m}_0 in terms of the eigenvectors of the covariance matrix (\mathbf{v}_j) .

As in MD, the initial weight vector is

$$\mathbf{m}_0 = \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix}$$

- plug into the Wyatt solution (Equation A.5) to obtain $\mathbf{m}(t)$.

$$\begin{aligned} C\mathbf{m}_0 &= \begin{pmatrix} \sigma^2 & 0 \\ 0 & \sigma^2 \end{pmatrix} \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix} = \sqrt{\frac{1}{2}} \begin{pmatrix} \sigma^2 \mathbf{v}_1 \\ \sigma^2 \mathbf{v}_1 \end{pmatrix} \\ e^{Ct}\mathbf{m}_0 &= \sqrt{\frac{1}{2}} \begin{pmatrix} e^{\sigma^2 t} \mathbf{v}_1 \\ e^{\sigma^2 t} \mathbf{v}_1 \end{pmatrix} \\ \|\mathbf{m}_0\|^2 &= 1 \\ \|e^{Ct}\mathbf{m}_0\|^2 &= e^{2\sigma^2 t} \end{aligned}$$

which yields

$$\mathbf{m}^{\text{BD}}(t) = \sqrt{\frac{1}{2}} \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_1 \end{pmatrix} \quad (\text{A.8})$$

Equation 3.3 implies that a neuron following Oja's rule, experiencing binocular deprivation following normal rearing, performs a random walk about the normal reared state.

Reverse Suture (RS)

- expand the initial weight vector \mathbf{m}_0 in terms of the eigenvectors of the covariance matrix (\mathbf{v}_j).

We run into an immediate problem if we try to use $\mathbf{m}^{\text{MD}}(t \rightarrow \infty)$ as \mathbf{m}_0 : the newly opened eye *never* recovers. To alleviate this, we assume that the monocular deprivation experiment did not achieve $t = \infty$, but just some large number T . In that case the initial weight vector for RS is

$$\mathbf{m}_0 = \begin{pmatrix} \mathbf{v}_1 \\ \epsilon \mathbf{v}_1 \end{pmatrix}$$

where $\epsilon \sim e^{(\sigma^2 - \lambda_1)T} \ll 1$

- plug into the Wyatt solution (Equation A.5) to obtain $\mathbf{m}(t)$.

$$\begin{aligned} C\mathbf{m}_0 &= \begin{pmatrix} \sigma^2 & 0 \\ 0 & C \end{pmatrix} \begin{pmatrix} \mathbf{v}_1 \\ \epsilon \mathbf{v}_1 \end{pmatrix} = \begin{pmatrix} \sigma^2 \mathbf{v}_1 \\ \lambda_1 \epsilon \mathbf{v}_1 \end{pmatrix} \\ e^{Ct}\mathbf{m}_0 &= \begin{pmatrix} e^{\sigma^2 t} \mathbf{v}_1 \\ e^{\lambda_1 t} \epsilon \mathbf{v}_1 \end{pmatrix} \\ \|\mathbf{m}_0\|^2 &= 1 \\ \|e^{Ct}\mathbf{m}_0\|^2 &= (e^{2\sigma^2 t} + \epsilon e^{2\lambda_1 t}) \end{aligned}$$

which yields

$$\mathbf{m}^{\text{RS}}(t) = \frac{\begin{pmatrix} e^{\sigma^2 t} \mathbf{v}_1 \\ e^{\lambda_1 t} \epsilon \mathbf{v}_1 \end{pmatrix}}{(e^{2\sigma^2 t} + \epsilon e^{2\lambda_1 t})^{1/2}} \quad (\text{A.9})$$

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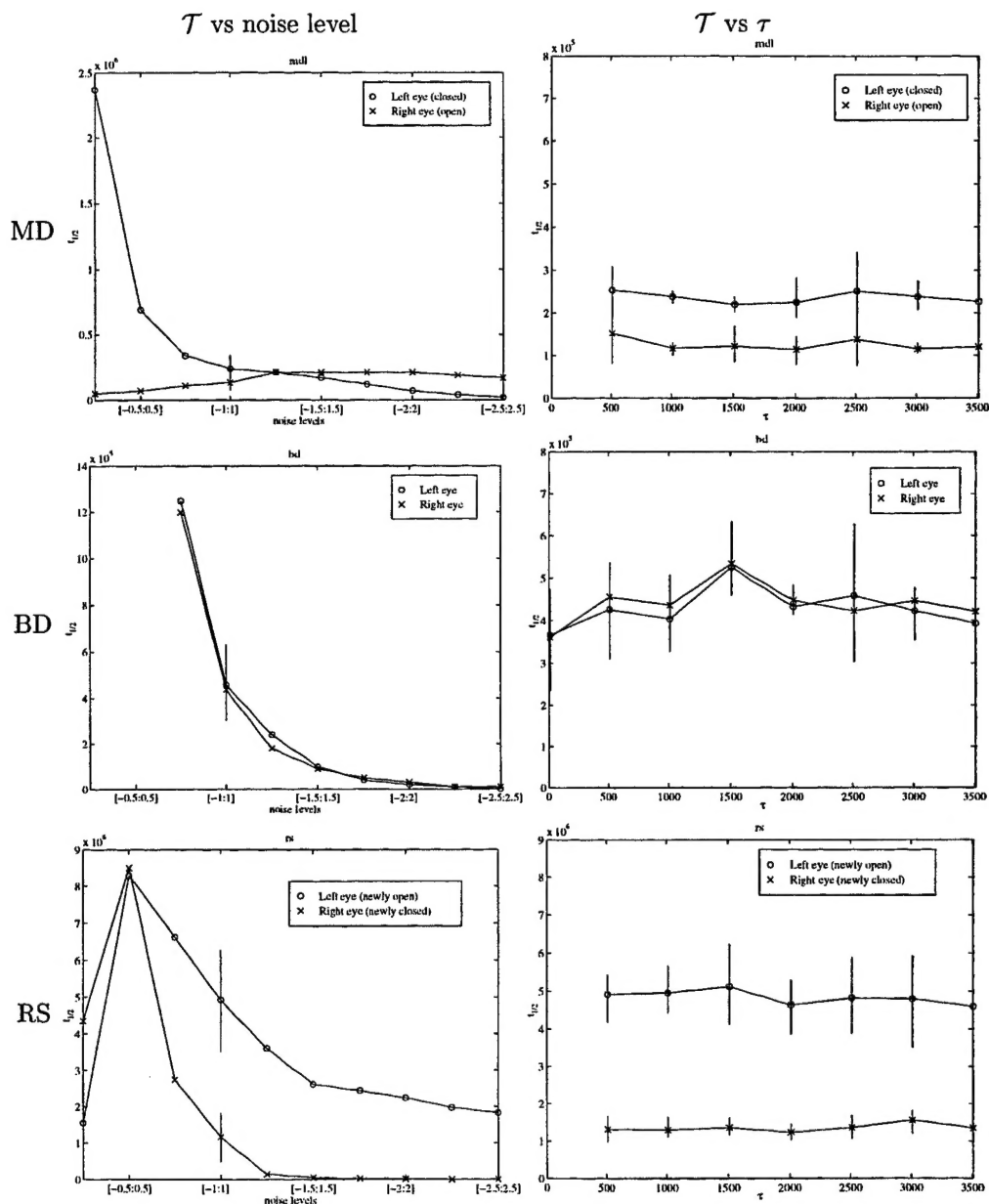


Figure 4: BCM Results: The effect of the noise level and memory constant τ on the response half-times of deprivation simulations, Monocular Deprivation (MD), Binocular Deprivation (BD), and Reverse Suture (RS).

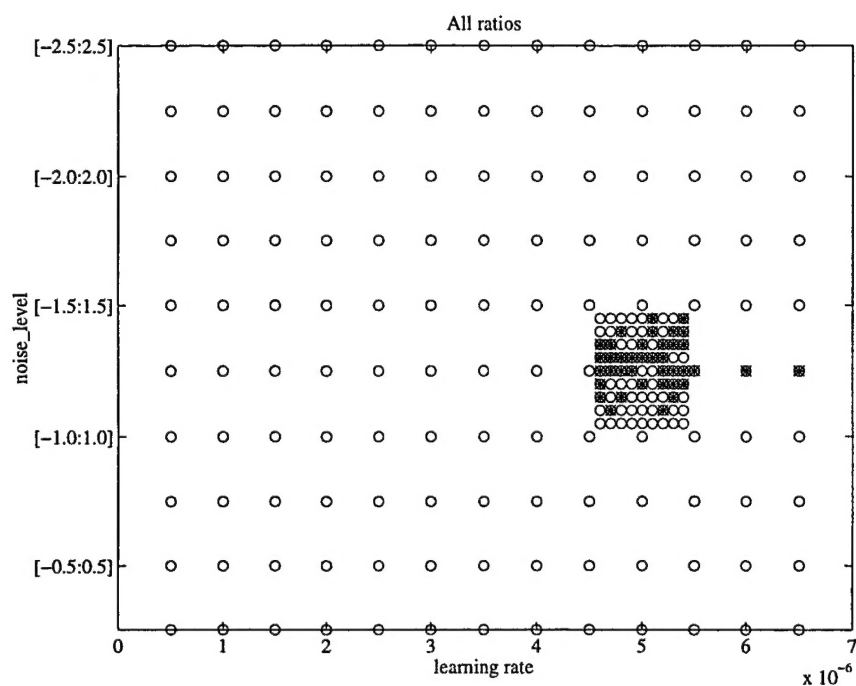


Figure 5: BCM Results: The valid parameter regime. Parameter points explored are denoted with o. Parameter points satisfying the experimentally determined time ratios are denoted with *. Note that the high density of points explored in one parameter region is a result of resampling around points where we found valid time ratios.